

Critical Review

ASSESSING THE RISKS OF PESTICIDES TO THREATENED AND ENDANGERED SPECIES USING POPULATION MODELING: A CRITICAL REVIEW AND RECOMMENDATIONS FOR FUTURE WORK

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Abstract: United States legislation requires the US Environmental Protection Agency to ensure that pesticide use does not cause unreasonable adverse effects on the environment, including species listed under the Endangered Species Act (ESA; hereafter referred to as listed species). Despite a long history of population models used in conservation biology and resource management and a 2013 report from the US National Research Council recommending their use, application of population models for pesticide risk assessments under the ESA has been minimal. The pertinent literature published from 2004 to 2014 was reviewed to explore the availability of population models and their frequency of use in listed species risk assessments. The models were categorized in terms of structure, taxonomic coverage, purpose, inputs and outputs, and whether the models included density dependence, stochasticity, or risk estimates, or were spatially explicit. Despite the widespread availability of models and an extensive literature documenting their use in other management contexts, only 2 of the approximately 400 studies reviewed used population models to assess the risks of pesticides to listed species. This result suggests that there is an untapped potential to adapt existing models for pesticide risk assessments under the ESA, but also that there are some challenges to do so for listed species. Key conclusions from the analysis are summarized, and priorities are recommended for future work to increase the usefulness of population models as tools for pesticide risk assessments. *Environ Toxicol Chem* 2016;9999:1–10. # 2016 SETAC

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INTRODUCTION

The US Endangered Species Act (ESA) was created to prevent the extinction of species and to allow species to recover to nonthreatened and/or endangered status [1]. The ESA is administered by the US Fish and Wildlife Service and the National Marine Fisheries Service, collectively called the Services. Currently close to 1600 species are listed as threatened or endangered in the United States, and over 2200 species are listed worldwide on the US Fish and Wildlife Service website. Overharvesting, habitat destruction, climate change, disease, invasive species, and pollution, among other factors, are believed to contribute to species declines and extinctions. Under the ESA, all federal agencies are required to ensure that their actions are not likely to jeopardize the continued existence of listed species or result in the destruction or adverse modification of critical habitat. For example, under the Federal Insecticide, Fungicide, and Rodenticide Act, the US Environmental Protection Agency (USEPA) is responsible for ensuring that registered pesticide use does not cause unreasonable adverse effects on the environment, including listed species and their critical habitats. Differences in the methods used by the USEPA and the Services to assess risk have contributed to lack of consensus on the risks posed by pesticides in some consultations for listed species.

In response to a request from the USEPA, the Services, and the US Department of Agriculture to review the different assessment

approaches, the National Research Council [2] recommended that a single common approach, based on the USEPA's well-established ecological risk assessment paradigm [3], be used across agencies. In a 3-step process, species of concern should be identified, with the first step based on simple estimates and conservative assumptions to screen out low-risk species from further consideration (i.e., to reach a "no-effect" determination by the USEPA). The next steps should become progressively more realistic, to determine risk for the remaining species and their habitats (i.e., step 2 would be used to reach a "not likely to adversely affect or likely to adversely affect decision" by the USEPA in consultation with the Services; and step 3 would be used to make a jeopardy decision by the Services).

A key conclusion of the National Research Council report was that population models are necessary to integrate effects of pesticides on survival and reproduction, to make jeopardy decisions for listed species. This is important because it encourages the USEPA and the Services to use a common approach for assessing risk, and it signals that risk assessments conducted under the ESA need to be closely aligned with protection of which are populations and species rather than individuals. In the present review population models are defined as mathematical or simulation models that make quantitative linkages between organism-level processes (e.g., survival, growth, reproduction, behavior) and population-level properties (e.g., population size, population growth rate, age/stage structure).

POPULATION MODELS AS TOOLS FOR ASSESSING RISK

Population models can be particularly useful for risk assessment under the ESA because they can integrate potential

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effects of exposure to pesticides on individual survival, reproduction, and growth, with relevant species-specific life history to project likely consequences for population persistence. Consequences for persistence can be assessed across larger spatial and temporal scales than is possible through field and laboratory studies. Population models are also useful for quantifying indirect impacts of pesticides (e.g., effects on supporting food webs of listed species). The National Research Council [2] concluded that population models are an appropriate framework for incorporating baseline conditions and projecting future cumulative effects into a risk assessment, both of which are important in a species jeopardy determination.

The National Research Council report stopped short of providing specific guidance on the application of population models. Although population models have a long history of use in conservation biology and resource management, their use in chemical risk assessments has been limited [4]. To gain a better understanding of population modeling and its potential role in assessing ecological risks of pesticides to listed species, CropLife America sponsored a science forum in April 2014 that brought together a diverse group of stakeholders with expertise in population modeling and/or assessing risks of pesticides to listed species. The outcome of the forum was a list of recommendations intended to assist government agencies in implementing population modeling in listed species assessments and to guide future research [5]. One of the recommendations for immediate action was a comprehensive review of existing population models to identify available models that could be used directly, or with minor modifications, in listed species pesticide risk assessments. Building on other reviews of the use of ecological models in risk assessment [6–9], we conducted such a literature review to fulfill 6 aims: 1) identify existing population models that have already been applied to assess risks of pesticides to listed species; 2) identify additional population models that have been used in other contexts that could provide useful approaches and/or data for listed species risk assessments; 3) categorize the models in terms of their coverage, structure, and processes included; 4) assess potential obstacles to using population models generally in ecological risk assessments and specifically for listed species pesticide risk assessments; 5) provide a database of published models that could be evaluated for use in

pesticide risk assessments for listed species; and 6) recommend priorities for future work to increase the usefulness of population models as tools for pesticide risk assessments.

Recent scientific opinions coming out of the European Food Safety Authority [10–12] and European Commission [13] suggest that population modeling is likely to play an increasing role in chemical risk assessments in Europe. Whereas our primary aim was to make recommendations that can assist with implementation of population modeling under the Federal Insecticide, Fungicide, and Rodenticide Act and the ESA, we believe that our findings are of relevance for risk assessments conducted under European legislation as well.

STRATEGY FOR THE LITERATURE REVIEW

We searched peer-reviewed English-language literature published during 2004 to 2014, using Web of Science, Google Scholar, and Scopus. We chose to focus on this period of research to reflect new developments since the publication of previous reviews on ecological models and their potential use in risk assessment [6–9]. We excluded gray literature because it may not be accessible for a wide audience, and because it is often not subject to independent peer review. Keywords included “population model” or “model”, combined with “conservation”, “endangered species”, “risk assessment”, “ecotoxicology”, “pesticide”, “indirect effects” or “cumulative effects”. Included in the review were population models that assess risks of pesticides or other stressors to nonthreatened and nonendangered species, as well as species listed under the ESA as threatened or endangered. We did not include models that assess only pesticide exposure or models that predict effects at the level of the individual only. We also did not consider empirical approaches (i.e., population monitoring) to assess risk of decline, nor did we include any studies dealing purely with statistical modeling and analysis of population data. Instead, our focus was on mechanistic effects models as defined by Preuss et al. [14] that produced outputs at the population level.

We summarized the characteristics of all models meeting the above criteria in a number of ways (Table 1).

We reviewed the models according to the level of structure represented in the population (Table 2). Scalar or unstructured

Table 1. Criteria used to categorize the models reviewed

Criterion	Options
Model type	Unstructured/scalar, matrix, individual-based model, other
Species	Latin name (common name)
Taxonomic group	Mammal, bird, fish, amphibian, reptile, aquatic invertebrate, terrestrial invertebrate, aquatic plant, terrestrial plant, generic
Species status	US listed (threatened or endangered, as of 17 August 2015), US not listed; harvested, invasive, pest, rare/protected, other
Stressors included	Chemical (pesticide, other organic/metal), physical (e.g., climate change, habitat loss), biological (e.g., predation, disease), harvest
Biological processes modeled (model inputs)	Life history, energetics, physiological process, movement/dispersal, behavior, population growth rate (scalar models only)
Model outputs (at the population level or above)	Biomass, abundance/density, structure, spatial distribution, population growth rate
Risk estimates	Probability of recovery/decline/extinction; time to recovery/decline/extinction
Model application	1¼ listed species AND pesticide; 2¼ listed species AND other organics/metals; 3¼ listed species and nonchemical stressor; 4¼ not listed species and pesticide; 5¼ not listed species and other organics/metals; 6¼ not listed species and nonchemical stressor
Sensitivity/elasticity analysis performed	Yes or no
Density dependence included	Yes (imposed, emergent) or no
Stochasticity included	Yes or no
Time horizon of model	None, up to 1 yr; up to 10 yr; up to 100 yr; > 100 yr
Spatial scale	Not spatially explicit; up to 1 m ² ; up to 1 ha; up to 10 ha; > 10 ha
Validation of model outputs	Field data, laboratory data, not validated
Exposure–effects link	Explicit (dose–response, toxicokinetic–toxicodynamic, etc.), implicit (hypothetical, probabilistic), not applicable
Source	Citation (author, year)

Table 2. Examples of population model types used in the present review^a

Model type	Generality	Realism	Accuracy	Definition	Reference examples for listed species
Unstructured/scalar	High	Low	Low	Differential equation formulations of total population abundance or density	[70–73]
Age-structured or stage-structured matrix	Medium to high	Medium to high	Medium to high	Matrix algebra formulations with discrete cohorts defined by age or life stage (e.g., egg, larva, pupa; or egg, juvenile, adult)	[17,74–76]
Individual-based model	Low	High	High	Computer simulation in discrete time steps with algebraic or rule-based expressions for the behavior and life history of a finite collection of individual organisms that interact with each other and their environment	[66,77–79]

^aScores for generality, realism, and accuracy are from Munns et al. [80].

models do not explicitly represent demographic differences among individuals or cohorts; these are formulated as differential or difference equations. Matrix models explicitly consider population structure, but only to a certain extent by representing distinct age, stage, and size classes, with no further distinction among individuals in each class being made. This class of models includes Leslie and Lefkovich matrices, and is often the core modeling approach in population viability analyses. Models explicitly representing individuals as discrete entities are individual-based models, in which population features typically emerge as a result of individual interactions, both intraspecifically and with environmental factors.

We further evaluated the types of stressors that were modeled, because many modeling studies were conducted for conservation or harvest management purposes. In addition, many listed species are exposed to nonchemical stressors (e.g., loss of habitat and overharvesting), which may influence how chemicals impact their populations. Whether or not density dependence was included in each model was also documented, because most natural populations are regulated in some way. We specifically looked to see whether density dependence on traits such as growth, reproduction, or survival was imposed by the use of some generic function such as implementing a population ceiling, or whether it was allowed to emerge from individual interactions and resource competition. We also tracked whether the models were stochastic, because stochasticity may reflect variation in ecological systems. We examined whether model outputs had been tested against independent data (i.e., not those data used for model calibration), which is especially relevant for risk assessment and decision-making, because models are required to represent species and populations of interest sufficiently well. Finally, we classified the models according to their published application, because we were specifically looking to quantify how many published modeling studies have already been used for pesticide risk assessment of listed species.

RESULTS OF THE LITERATURE REVIEW

The literature search, applying our keywords and criteria defined above, resulted in 403 relevant studies that we reviewed in detail (see the Supplemental Data). In summarizing the characteristics of the reports, it should be noted that the same study could be listed more than once (e.g., if the same study included more than 1 model type, multiple species, or multiple stressors). Of the 403 studies represented in our analysis, the vast majority (66%) used matrix models; 15% used individual-based models; 12% used other types of structured models; 6% used unstructured models (e.g., differential equation models); and 1% included more than 1 model type. Of the 440 species that

were represented in the models, 23% were US listed species; 33% were nonlisted US species; 22% were species that are considered rare or protected in other jurisdictions; 5% were harvested species; 6% were pest/invasive species; and 11% were species not falling into any of these categories.

Terrestrial plants (dicots, monocots, and nonangiosperms combined), mammals, and birds were the most modeled taxonomic groups, followed by fish, aquatic invertebrates, and terrestrial invertebrates. There were relatively few models of amphibians and reptiles and only 2 models of aquatic plants [15,16] (Figure 1A).

In Figure 1B, we present the number of models including different stressors. Of the 403 studies included in our analysis, 9% included pesticides as stressors, and another 10% assessed the effects of other chemical stressors. A total of 38% of the studies were focused on effects of physical stressors (such as habitat loss), another 6% considered biological stressors, 9% modeled the effects of harvest, and 19% considered effects of multiple types of stressors. In 9% of the studies, either the stressor was unknown or theoretical, or there was no explicit inclusion of stressor impacts. Of the 108 studies including some kind of chemical stressor, 36 (33%) used a dose–response function to model the chemical effects; 19 (18%) represented the effects using a mechanistic exposure–effect model such as TKTD or DEBtox; and 13 (12%) used empirical laboratory data (i.e., modeling only the concentrations and effects that were tested in the laboratory experiments). In 36 of the studies (33%), chemical effects were modeled implicitly (i.e., by considering hypothetical impacts on vital rates), and 4 (4%) studies did not report a chemical effect (see the Supplemental Data).

Life-history information, movement (dispersal and migration), and physiological processes were the most represented biological processes included as input variables in the reviewed models (Figure 2A). Some measure of population abundance or density (48% of the model outputs) and population growth rate (33% of model outputs) were by far the most common model outputs, with population structure and spatial distribution also represented (9% and 4% of the outputs, respectively; Figure 2B). It should be noted that unstructured models sometimes used population growth rate as an input variable, whereas for all other classes of models population growth rate was an output variable. Fifty-seven percent of the studies included explicit risk estimates, the most common being probability of extinction, decline, persistence and time to extinction, decline and/or recovery. Fifty-three percent of the studies included density dependence, 71% included stochasticity, and 46% were spatially explicit. Furthermore, 257 of the 403 studies (67%) included sensitivity analyses, whereas only 82 (20%) included some form of partial or comprehensive model validation (data not shown).

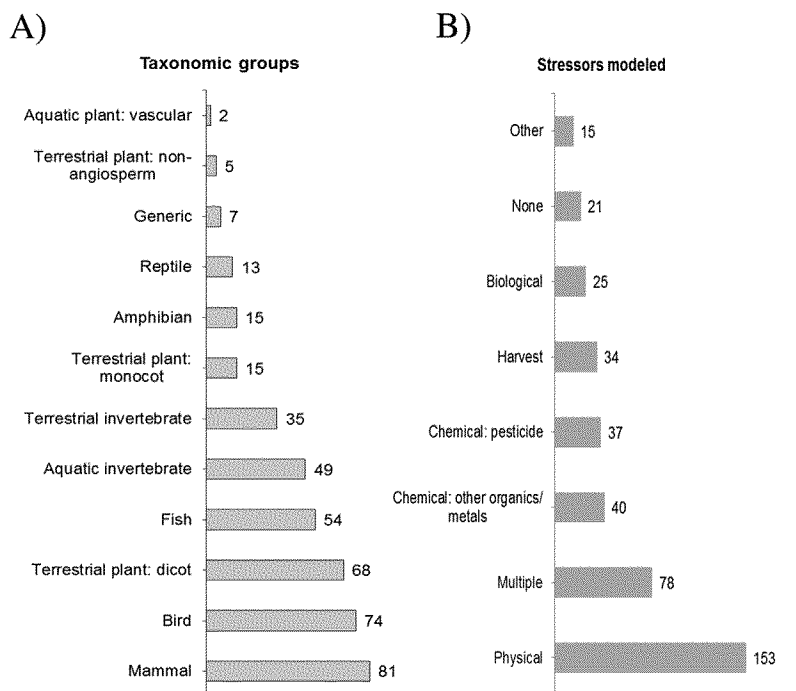


Figure 1. Representation of taxa and stressors included in our model review. (A) Number of species distributed across taxonomic groups. (B) Number of models including different types of stressors (of the 78 studies containing multiple stressors, 31 included chemicals: 21 pesticides and 10 other chemicals). Because some models included multiple taxa and/or multiple stressors, the totals are greater than the number of studies reviewed.

We found only 2 studies published in the peer-reviewed literature during the last decade that used population models to assess the risks of pesticides to listed species, and both of these were for salmon (Figure 3). Baldwin et al. [17] assessed the impacts of organophosphate and carbamate insecticides on ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). Macneale et al. [18] modified the model of Baldwin et al. [17]

to assess the importance of direct versus food-web-mediated impacts of these pesticides on the species.

We found 7 additional studies that used population models to assess the risks of other toxic chemicals to listed species and 2 reports that explored the effects of pesticides on species that have been delisted. Most of these studies were also concerned with salmonids. In these studies, population models were used to compare the effects of stress from chemicals for different life histories as observed in salmonids or other fish species. The toxicants were often modeled hypothetically (i.e., by simulating defined reductions in survival rates of each life stage) [19–22]. Mebane and Arthaud [23] and Spromberg and Scholz [24] explored the effects on 1 life stage (growth of juveniles) and mortality of prespawning adult salmon, respectively, for population-level responses. Three more studies addressed impacts of chemical exposures on birds. Finkelstein et al. [25] modeled the effects of lead poisoning on recovery of the listed California condor (*Gymnogyps californianus*). The delisted Peregrine falcon (*Falco peregrinus*) was addressed in

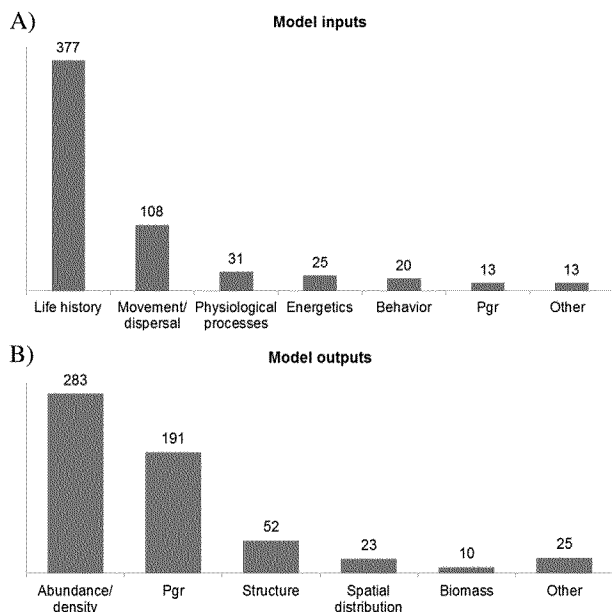


Figure 2. The reviewed studies classified by (A) model inputs and (B) model outputs. The majority of models assessed multiple processes (i.e., input variables) and predicted multiple outputs, resulting in a total greater than the actual number of studies reviewed. Population growth rate was only used as an input variable in scalar models; in all other model types, population growth rate was an output variable. Pgr = population growth rate.

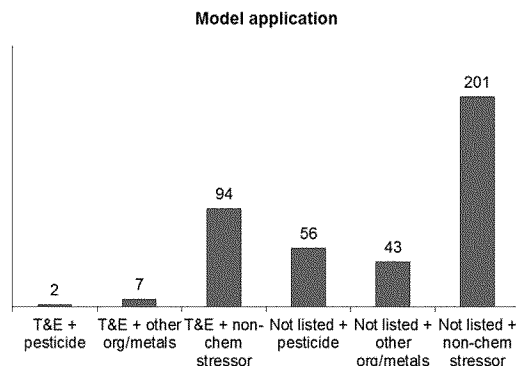


Figure 3. Number of models reviewed according to the application for which they were used in the original publication. T&E = threatened and endangered.

2 publications [26,27]. In both studies, population responses to DDT exposure were assessed. All 9 of the above studies used a matrix modeling approach, none were spatially explicit, 7 of the 9 imposed density dependence, and 2 of the 9 included stochasticity.

Despite the paucity of population models including both listed species and toxic chemicals, there were many more models that included one or the other. We found a total of 94 publications describing population models of listed species (but not chemical stressors; plus the 2 studies for delisted species), 57 publications with population models designed to test the effects of pesticides on nonlisted species, and 44 publications modeling the effects of other chemicals on nonlisted species. Some of these studies contain relevant life-history and other data for listed species that could be highly valuable for adapting models to explore pesticide effects. Others may be valuable for providing exposure-response information for toxic chemicals and species that could provide useful toxicological surrogates for listed species. In addition, there were 199 publications in our database containing population models for nonlisted species and for which the stressor was not chemical or that did not explicitly explore the effects of a stressor. These studies provide a good overview of the kinds of population modeling approaches that have been conducted over the last decade.

It is apparent from our analysis that there exists a wide variety of options for population modeling based on different analytical or simulation techniques, model platforms, and software. Stage-structured or age-structured matrix models remain the most common approach to population modeling. These vary from very simple, deterministic, density-independent models to more sophisticated, stochastic models that incorporate various kinds of density dependence. It should be noted that matrix models project expected population dynamics based on estimated vital rates (with or without density dependence) [28], whereas most individual-based models aim to predict vital rates and consequent population dynamics based on individuals' interactions with their environment and each other [29]. The more recent literature has seen an increase in the development and application of spatially explicit individual-based models. This is likely because of advances in computational power, as well as efforts by the modeling community to develop guidance for developing, testing, and communicating these kinds of models [30–33]. The major advantages of individual-based models for pesticide risk assessment are that they interface well with spatially and temporally varying exposure information [34], are able to include specific behaviors that affect risk [35], and can be scaled up to cover large landscapes if necessary [36]. In comparison with matrix models, it is more common for the outputs of individual-based models to be tested against independent data (we found validation efforts reported for 10% of the matrix models, and for 52% of the individual-based models). Pattern-oriented modeling [30] allows comparison of multiple individual-based model outputs against independent data, increasing the possibilities for model testing [29,35–37]. A particularly good example of model validation within the context of pesticide risk assessment is provided by Wang [38].

In summary, despite the widespread availability of modeling approaches and an extensive literature documenting the use of population models to address either species management questions or impacts of chemicals on populations, only 2 of the approximately 400 studies that we reviewed used population models to assess the risks of pesticides to listed species. This result suggests that there is an untapped potential to adapt

already well-developed models for pesticide risk assessments under the ESA, but also that there are some important obstacles for developing and using such models. Comprehensive life-history and ecological information on many listed species may currently limit the development of detailed species-specific population models for listed species. However, the models that were applied to listed and unlisted salmonids and other fish species [17,19–24] show the benefit of relatively simple models in comparing the vulnerabilities of species with different life-history traits. This can help in prioritizing species for further assessment and guide efforts for additional data collection. Moreover, a key advantage of individual-based models is that they may be based on principles of fitness maximization by individual organisms and thus do not necessarily require precise estimates of life-history traits [39].

LIMITATIONS OF CURRENT EFFECTS ASSESSMENTS AND IMPLICATIONS FOR POPULATION MODELING

Toxicity data for pesticides are generally only collected for a handful of test species. Accordingly, toxicity data are not available for most species, including listed species, which may potentially be exposed to a pesticide. There are established methods for interspecies extrapolation of toxicity data from standard test species to untested species [40,41]. However, toxicological data are often not measured in a way that is most useful for integrating into population models. As noted by the National Research Council report, pesticide effects should be estimated at a range of concentrations that includes all values that the population might reasonably encounter. However, test results are often expressed as threshold values or point estimates—such as the no-observed-effect concentration (NOEC), the lowest-observed-effect concentration (LOEC), and the median lethal concentration (LC50)—which do not provide adequate information for a population-level risk assessment [2]. This is not a criticism of using models but rather underlines that if we want to use toxicity data to inform likely impacts on populations, we ought to be reporting the data in a way that is useful for assessing population-level impacts. Notwithstanding the limitations of existing data packages, when one has a NOEC and an LC50, it is possible to make some conservative assumptions (i.e., linearly interpolate effects between the NOEC and LC50 and assume 100% effect above the LC50). The point is that these are limitations on the kind of data collected to conduct risk assessments and not limitations of population modeling.

Although implicit in the use of organism-level toxicity data in effects assessments, it is invalid to assume that responses at the organism level are directly proportional to responses at the population level. As a number of reports in our review demonstrate, the same potential effects (of chemicals and other stressors) at the organism level can have vastly different consequences at the population level in different species [22,42]. For example, certain effects of toxicants for a population can exceed the effects observed in individuals [43], or may be lower [44]. Potential population-level effects may also change depending on other factors in the model (e.g., population density [27]). Different mechanisms lead to variation in population-level outcomes, such as including variation in life-history traits [19], combining lethal and sublethal effects [45], density dependence [46], or temporal and spatial exposure patterns [47]. Population modeling can provide quantitative extrapolation of organism-level effects to the population level that accounts for differences in species life history and ecology.

Population models, whether they are simple, generic approaches or complex, species-specific models, can be used to explore the effects of changes in the processes they represent, including life-history traits, sensitivity to toxicants, exposure patterns, environmental conditions, and many more. If data gaps exist, population models can yield insights into the importance of the processes in the context of a pesticide risk assessment. The models can also be used to assess the effects of variance in empirical datasets on population-level responses, and make it possible to conduct so-called experiments that are virtually impossible to conduct in the field because of the effort or time such experiments would take.

In addition to using population models as tools to gain insight into the effects of uncertainty in empirical data, our review indicates that methods exist for dealing with data gaps, and these include allometric estimation of vital rates [48], Bayesian techniques [49], use of surrogate species ([50]; but see Spromberg and Birge [19] and Banks et al. [22,51]), and iteration of unknown parameters based on initial values of population statistics (e.g., growth rates) [28]. In the present review it is important to note that gaps in data and understanding exist for traditional approaches to risk assessment. An advantage of the models is that they make these gaps explicit, rather than hiding them behind an assessment or uncertainty factor.

For making quantitative predictions of future population sizes or growth rates of specific populations in particular habitats, species-specific models that incorporate substantial ecological realism may be necessary. For example, factors such as species distribution (continental vs island endemic) can influence the kinds of constraints that species face, and these need to be considered and appropriately captured in the models. Species-specific life-history and ecological data necessary to parameterize and evaluate population models can be challenging to collect [36], and this can be particularly important when one is attempting to validate very complex, species-specific models against data representative of field populations of concern [36,52]. In such situations, comprehensive analysis of the models is crucial to determining the relative importance of included factors and processes [53]. This is not only a test for the reliability of the models [32,33], but also helps to prioritize future data collection efforts [52], and can inform management strategies and postmanagement monitoring efforts [54].

SPECIAL CONSIDERATIONS FOR LISTED SPECIES ASSESSMENTS

A general problem for risk assessments of listed species is lack of data on toxicological responses, key life-history traits, and ecological characteristics. There is limited evidence to suggest that some listed species are toxicologically more sensitive than nonlisted species [55], and when listed species are taxonomically distant from taxa for which toxicity data are available (e.g., corals), more conservative assumptions about toxicological sensitivity could be made. Even when data are available, they may be less certain because of small sample sizes, limited number of studies, and so on. Population models can help to address these points in various ways. For example, population models can provide insight into the relative importance of different biological processes, for instance, the vulnerability to toxic stress of species dependent on their life-history traits [19,22,45,51]. Such applications make validation of population models with field data a lesser concern. Even simple and fairly generic models can be of great value for the identification of species of most concern within a taxonomic

group and for selecting appropriate surrogate species [56]. In addition, generic (rather than species-specific) approaches can be used to integrate combined lethal and sublethal effects on populations [18,45,46,57], and can guide the focus for more detailed assessments, including more complex population models, field data collections, or other sources of information. Moreover, although most decision makers would like to see models validated by testing their predictions with new experiments or data, this is neither sufficient nor necessary for a model to be useful for decision support [33].

In the context of screening out low-risk situations, species-specific effects thresholds derived from population models could provide an alternative to extremely conservative general thresholds based on individual-level effects. For example, a standard threshold for listed animal species of a 1 in a million chance of acute mortality based either on the most sensitive species or on the 5th centile chronic NOEC from a species sensitivity distribution has been proposed at step 1 of the 3-step interim process described above to distinguish between “no effect” and “may effect” [58].

Given the variety of species life histories and differences in objectives of the different steps of the consultation process, it is likely there is no 1 best population-level endpoint or risk expression for assessing population risk. Whereas population growth rate is 1 of the most commonly used metrics and can provide information on likely rates of recovery or decline, there is some evidence that long-term population size is more informative, more sensitive for predicting population performance, and more easily understood and valued by the public [29]. In some cases exposed populations are predicted to stabilize at similar growth rates as unexposed populations but at a lower population size [59,60], and all else being equal, smaller population size means a higher risk of extinction because of demographic and environmental stochasticity and catastrophic events [61]. Explicit estimates of extinction risk are intuitively attractive, because they are more relevant to protection goals; however, they have been shown to be sensitive to small errors or uncertainties in model parameters [23]. It has therefore been suggested that expected minimum population size [23], decline in population size relative to unexposed populations [29], or relative extinction risk among populations [62] are less sensitive to model uncertainties or stochastic variability and may therefore be more robust indicators of population status than expressions of absolute extinction risk. In addition, the precision of model outputs is also a key factor to consider when one is using models for regulatory decisions. Instead of limiting the outputs of population models to a single endpoint, we recommend analysis of multiple endpoints (e.g., population growth rate, population size, and a measure of decline or extinction risk), because the most sensitive measure may depend on the conditions of the modeled population.

The National Research Council [2] concluded that density dependence should be incorporated into population models for listed species. Density dependence is a prevalent feature of population dynamics found even in rare species [63] that has been shown to interact with effects of chemicals, with examples of both more-than-additive and less-than-additive interactions in the literature [64]. Approximately half of the model approaches reviewed in the present study included density dependence. Some modeling approaches require that assumptions about the form of density dependence be imposed on the model, either by defining population ceilings [65], by defining specific forms of density dependence impacting

life-history traits [19,27,59], or by assuming additive impacts on individual survival [47,54]. In others, density dependence emerges from intraspecific competition for a limiting resource [14,35,66]. Either way, decisions about how to include density dependence need thoughtful consideration, because density dependence can interact with chemicals in different ways, with contrasting consequences for population persistence. The present review suggests that, in some cases, density dependence is likely to reduce the impacts of low exposures to pesticides (and other stressors) at the population level [19,27,65]. Removal of organisms releases the rest of the population from competition, and a subsequent increase in vital rates compensates for initial adverse effects of chemicals. However, in some studies no impacts of density-dependent regulation on population-level effects of chemicals were detected [47]. In others, impacts of density dependence were exacerbated in the presence of chemicals [47,59]. When, for instance, reproduction is density-dependent and further compromised by chemical exposure, impacts at the population level may exceed what either density dependence or chemicals had in isolation [59]. In addition, populations exhibiting pronounced spatial heterogeneity in some aspect of their life history (e.g., when density of certain life stages is very high in some parts of the habitat) may also experience magnified impacts of chemicals in the presence of density-dependent mechanisms targeting those life stages [47]. To correctly capture the dynamics of populations exposed to chemicals, regulating mechanisms need to be carefully considered and included. Data-driven empirical and mechanistic approaches, rather than generic functions, may be a more realistic approach to implementing density-dependent functions into population models [67].

PRIORITIES FOR FURTHER ACTION

To ensure that model users and assessors understand a model's strengths and limitations as well as its domain of applicability, we recommend that further attention be devoted to ensuring standard documentation and model evaluation and that these be included in future guidelines for ESA framework implementation. Decisions about model assumptions, which and how processes are represented in the model, model parameterization, and calibration need to be made based on available data and knowledge. Comprehensive sensitivity and uncertainty analyses have to be conducted to assess the reliability of a model [32,33,68]. Most of the models in our review (67%, or 257 of the 403 studies reviewed) included some kind of sensitivity analysis, although the scope of the analyses varied widely from testing the impact of varying a single parameter within a small range to a more comprehensive exploration of the parameter space and interactions between factors. The responsiveness of the model to chemical and nonchemical stressors should be evaluated (i.e., similar to a positive control [toxic standard] in laboratory and field toxicity studies). Ideally, the modeler should also explore the consequences of leaving out certain factors or processes. If possible, validation of output with independent data should be conducted, as was the case for 20% of the studies we reviewed; it was often not clear whether the data used for the validation efforts were actually independent of the data sources used during model development and calibration. This needs to be made very clear. Rigorous documentation of all steps in model development and application is essential for the transparency of any approach. Without documentation, it cannot be determined

whether a model is a useful tool in the context of an assessment, and under which conditions the results of the model are applicable [32,68]. Case studies can increase confidence in the reliability and relevance of models, for example, by the use of multiple modeling approaches for the same species, validation of models using data-rich nonlisted species, and regular confirmation of model predictions with field monitoring studies.

Given the large number of listed species, there is a need to prioritize species for in-depth risk assessments. In our view, population models can therefore have a role to play in all steps of the 3-step interagency consultation process described in the Introduction. Even within a narrow taxonomic group, variations in life-history traits can result in vastly different population-level outcomes of organism-level responses to toxic stress [22,51]. Modeling approaches can be applied to identify the most vulnerable species within a group by comparing different life-history types [19,56]. Assessing species groups rather than individual species may allow focus on a subset of groups and identification of the most vulnerable species within the groups for further, detailed assessment. It is currently not feasible to assess risk to several hundred species 1 by 1 in each risk assessment. If a subset of species can be identified as most vulnerable because of their potential for exposure, life-history traits, and/or sensitivity to a pesticide, an ecologically relevant risk assessment can be conducted for those species that is still protective for all listed species. In addition, there is a pressing need for guidance on how model choice and model development for pesticide risk assessment should be approached in the light of data availability and species traits. Major concerns remain about the lack of ecological and toxicity data for listed species. Clearly, having some understanding of the factors that have driven populations of listed species into decline or rarity is important for assessing risks of further decline or lack of recovery. There are mixed views on whether and how data from surrogate species are helpful for model development. Kesler and Haig [50] argue for using surrogate species to develop population models for listed species when data for the latter are missing. Banks et al. [22,51] and Spromberg and Birge [19] highlight that care needs to be taken when one is identifying toxicological surrogates because of the importance of life-history differences on population-level impacts. As mentioned in the section Limitations of current effects assessments and implications for population modeling, this is the case for all species (not just listed species). Thus, the use of surrogate species is the norm in chemical risk assessments of nonlisted species and underlines why population models are needed to integrate toxicological data on individual-level endpoints into likely impacts on populations as part of the interspecies effects extrapolation. Given that many listed species lack ecological and toxicological data, surrogates will undoubtedly need to be identified for some species. Species groupings discussed in the section Special considerations for listed species assessments and toxicokinetic and/or toxicodynamic modeling [69] could support identification of surrogates and toxicity extrapolations [40], and more data on the life history and ecology of listed species are needed to improve modeling results. In the meantime, the models can be used to quantify the effects of uncertainties in life-history traits and toxicant sensitivities of listed species. Knowledge about what factors have driven the decline of the species in question is especially important for developing species-specific models to assess whether pesticides add to the existing risk of further population decline or lack of recovery. Such knowledge may also aid selection of adequate surrogate species.

The studies that we reviewed include examples of simple, deterministic population models as well as more sophisticated models that include stochasticity, density dependence, and spatial and/or temporal variability in exposure and effects. The degree of complexity that needs to be included in models will depend on whether realistic effect sizes of population-level outcomes are needed or whether qualitative assessments of relative risk or importance of traits are sufficient. Although lack of data on listed species may initially limit the level of detail that can be included in models, collecting such data should be a high priority under the ESA.

In summary, population models can benefit pesticide risk assessments for listed species at all steps of the process by providing ecologically informed effects thresholds, identifying the key drivers of species decline and recovery for more effective management, assessing the relative vulnerability of species to pesticides and other stressors, prioritizing species for model development, integrating effects of pesticides on lethal and sublethal responses as well as integrating effects of multiple stressors and indirect effects, exploring population-level impacts at temporal and spatial scales that are difficult to assess empirically, and improving the design and reporting of toxicity tests. The intent of the present review is to assist the USEPA and the Services with further development and implementation of population modeling in future ecological and listed species risk assessments for pesticides. It is beyond the scope of the present review to answer all questions related to implementation of population models for risk assessments of listed species or to provide a detailed decision framework for integrating models into the existing multistep process. However, we believe that the insights gained will be useful for implementing population models in this and other jurisdictions and applications that extend beyond the ESA and pesticides, and we hope that the compiled database will provide a useful resource for further work in this area.

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